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MODELE MATHEMATIQUE DE LA POLLUTION EN MER DU NORD.

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A simple simulation model for the phytoplankton spring bloom in the Sluice Dock at Ostend.

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I.Introduction.

The Sluice Dock at Ostend is a system kept isolated from the sea for about six months and where water motions are limited.The synecological study of the Dock was started in 1971(Podamo ,1974)

All this makes it a particularly good subject for a mathematical simulation of biological phenomena.

This particular model works without zooplankton.The interaction between phytoplankton and zooplankton (with its two antagonistic aspect:grazing and stimulation of growth by excretory NH_4)seems to occur mostly after the single species bloom(Kommaerts-Billiet,Kommaerts,Daro,1974).

Hence there must be another mortality cause than grazing. We consider this as natural mortality, and its relationship with the growth constant taken as an index of health is one of the major hypotheses in the model.
The seasonal variations of inorganic nitrogen concentration in water and the marked effect of addition of it on photosynthesis rates make us believe that N nutrients are controlling phytoplankton growth. NH_4^+ particulary is believed to play a major role since nitrate reductase activity is likely inhibited at the concentrations observed (Eppley et al 1969). On the other hand denitrification mecanisms in the sediment layer require most of the dissolved NO_3^- from water (Billen pers. comm.).
The model was elaborated taking into account the conditions prevailing in the Sluice Dock at the time of the closure of the sluices. The only forced variation in the model is the climatic one (incident light and water temperature).

As contrasted with many simulation models, the time scale is short (one hour instead of one day). This originates from the observations made during 24-hours periods when several parameters were demonstrated to vary strongly. Attempts to simulate these variations led to the actual model.

II. Biological functions.

All functions are integrated numerically with dt=1hour.

II.1. The dB/dt function

$$\frac{dB}{dt} = (k-m-r-e)B$$

where B = biomass of phytoplankton

t = time

k = growth rate

r = respiration rate

e = excretion rate

II.1.1. The growth rate k and the light-photosynthesis relationship.

The actual k constant is evaluated relative to an optimal k (i.e.for optimal light): 1°) defined after saturation kinetics(Michaëlis-Menten) and at I2°C.

$$k_{I2} = \frac{k_{max} \times N}{k_s + N}$$

where N = concentration of inorganic nitrogen in water

k_{max} and k_s = saturation parameters defined at I2°C.

2°) corrected for temperature differences (Arrhenius law)

$$k_T = k_{I2} \times Q_{I0}^{(T-I2)/I0} = k_{opt}$$

so that k_{opt} x B = optimal gross production (p_{opt})

For a given irradiance , $k = k_{opt} \times f(I'_o, I'_K)$

where $f(I'_o, I_K)$ is a Vollenweider (1965) function. The variables are incident light (I'_o),water transparency (η) and specific parameters such as I'_K and photoinhibition coefficients α and n.

The link between the Michaëlis-Menten kinetics and the Vollenweider model reflects on the equation for I'_K . One supposes that the initial slope of the light-photosynthesis relationship is constant so that

$$I'_K = \frac{k_{opt}}{C1}$$

II.1.2. The mortality rate

An inverse relationship is assumed between k_{opt} (taken as an index of health) and m : $m = C_2 / k_{opt} + C_3$

However not demonstrated for phytoplankton , this kind of relation is expected to show some generality. It seems to us to be more realistic than the sole statistic function of biomass

$m = C_3$ used by some modellers.

II.1.3. The respiration rate

The respiration rate is taken proportional to the phytoplankton biomass . Indeed, fluctuations mentioned in the literature are relative to photosynthesis and are likely related to photosynthesis variations rather than to true respiration variations.

$$r = C_4$$

The influence of temperature is simulated here :

$$r_T = r_{I2} \times Q_{I0}^{(T-I2)/I0}$$

II.1.4. The excretion rate

One is supposing that 1) the maximal excretion rate is a function of biomass. The reasoning is similar to that used for the respiration rate

$$e_{opt} = C5$$

2) however , there is also some relation to gross photosynthesis (Tanaka , Nakanishi and Kadota, 1974) so that the vertical profile of excretion has the same shape as that of photosynthesis . We use the proportionality :

$$\frac{e}{e_{opt}} = \frac{p}{p_{opt}}$$

II.2. The dN / dt function

II.2.1. Nutrient uptake

$$-\frac{dN}{dt} = \frac{1}{7} \times \frac{dB}{dt}$$

Carbone fixation and nitrogen uptake rates are supposed to be proportional so that the C / N ratio in phytoplankton (about 7, Strickland 1960) should not change (Podano, 1974). This N uptake is related to gross organic C production in this model (the net fixation of N being proportional to net organic carbon production , and the excreted N

corresponding to excreted C + respired C.

II.2.2. Regeneration via the phytoplankton excretions and the heterotrophi bacteria

Metabolization by the bacteria would affect about 30% of e (Steele, 1974), the other 70% beeing presumably mineralized.

So that : $\frac{dN}{dt} = \frac{1}{7} \times (0.7 \times (e + r)) \times B$

II.2.3. Regeneration by the sediment

A constant rate of NH_4^+ regeneration is assumed (Podano, 1974).

(average = 5 mg $N\text{-}NH_4^+ / m^2/h$)

This rate is temperature dependent : $rate_T = rate_{12} \times Q_{10}^{(T-12)/10}$

II.3. Feed-back biomass-water transparency

One has observed in the Sluice Dock at Ostend that the relation

$\eta = 1 + (65.10^{-5} \times B)$ satisfied to most cases.

III . The forced functions : the climate

The simulations of annual or daily variations of light or temperature are made after the observed variations in the Sluice Dock.

III.1. Light

The annual variation (average) of midday maximal P.A.R. irradiance ($I'_{o\ max}$) and of daylenght (λ) has been simulated :

$$I'_{o\ max_j} = 60 + 44 \left(\sin \frac{2\pi(j-80)}{365} \right)$$

$$\lambda_j = 12 + 4 \left(\sin \frac{2\pi(j-80)}{365} \right)$$

Similarly , the diurnal curve is simulated by the equation :

$$I'_{ot} = I'_{o\ max_j} \cdot 0.5 \left(1 + \cos \frac{2\pi t}{\lambda} \right)$$ (Vollenweider,1965)

III.2. Water temperature

The annual variation of mean daily temperature is simulated by :

$$\overline{T}_j = 11.5 + 8.5 \left(\sin \frac{2\pi(j-120)}{365} \right)$$

The daily variation is simulated by :

$$T_t = \overline{T}_j + 1.5 \left(\sin \frac{2\pi(t-9)}{24} \right)$$

IV. Results and discussion.

IV.1. A system with damping oscillations (fig.1)

The output of the model happened to be an oscillating system, the first peak of which simulates the spring bloom. The relation phytoplankton-nutrient is indeed at first sight comparable to a prey-predator system.

However, a fundamental difference with the Lotka-Volterra or Leslie equations is that the "prey" regeneration rate is independent of "prey" density.

The equations set for a simplifyed model would then become:

"prey"(=nutrient) $\frac{dx}{dt} = a - cxy$ (instead of $ax - bx^2 - cxy$)

"predator"(=phytoplankton) $\frac{dy}{dt} = -ey + cxy$

or, fitting the Michaëlis-Menten relationship in:

$$\frac{dx}{dt} = a - \frac{Cxy}{k+x}$$

$$\frac{dy}{dt} = -ey + \frac{Cxy}{k+x}$$

The solutions of both sets show conservative oscillations.

The damping in the simulation model results from the several feedbacks added to the system and from the climate variation. The system trajectory in the phase plane (fig.1A) becomes a spiral converging towards a stationary point (=control by the sediment). Thus the system is stable however the equilibrium point is slowly moving in the plane as the climate conditions are changing.

IV.2. Testing the model for various parameters (figs. 2, 3)

Various scenarios involving different I'_k (fig. 2 A), K_s (fig. 2 B), mortality coefficient C_3 (fig. 2C), annual temperature curve (fig. 2 D), annual incident light curve (fig. 3 A) show comparable effects:

- a parameter enhancing primary production leads to an early small bloom and a quick exhaustion of the limiting nutrient.
- a parameter slowing primary production leads to a temporary accumulation of the nutrient supply, followed by a much more important outburst of phytoplankton.

The system proved to be very sensitive to small changes in I'_k or light input as compared to changes of half-saturation constants. Mortality also exerts a very important influence, a variation of the minimum rate (C_3) having non-linearly related effects on the system.

An improvement on the deterministic model is the introduction of a stochastic variation of the daily energetic input, as an attempt to simulate the natural fluctuations of the light climate. The result is an obvious shift in time of the blooming periode, (fig. 3 c) and an increased sensitivity (hence fragility) of the ecosystem. The stochastic variation is comprised between the upper and lower limits observed in nature and simulated by:

$$I'_{o\,max} = 87 + 50 \left(\sin \frac{2\pi (j-80)}{365}\right)$$

$$I'_{o\,max} = 28 + 22 \left(\sin \frac{2\pi (j-80)}{365}\right)$$

The explanation for these disturbances is that, however the average daily light would not change, the saturation kinetics make that production is relatively more affected by low light intensities. In a stochastic light model, the trigger effect of a short sequence of beautiful days is also evident.

IV.3. Conclusion.

However this model is still simple and suffers the usual assumptions (i.e. no delayed feedbacks etc.) made in modelling, the variation predicted on partly theoretical grounds is not unlike that observed in nature, as far as the first oscillation is concerned (fig. 4) and however further adjustments are needed.

Some parameters are demonstrated to be particularly important: I'_k , mortality coefficient and light input. The strong influence of the light climate was further emphasized in stochastic and real light climate simulations. After the first peak, interferences with growing zooplankton would lead to departures from the stable equilibrium predicted in this model. Such a model has already been tested and will be published very soon.

In contrast to equations that merely conform to the observed phenomena, this model is an attempt of description of the Sluice Dock ecosystem that has some justification in terms of the known or postulated behaviour of the components of the system. We consider it as a first framework with the aim of refining our knowledge of these behaviours and testing the many hypothesises it is depending on.

Appendix : late modifications of the model are :

1. Nitrogen uptake is related to net production
2. A lower C/N ratio is used (=5.5 , after the review of Banse, 1974).

Both modifications do not alter the conclusions of this report .

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Initial conditions and constants

Biomass $B = 78$ mg C/m^3

Ammonia $N = 300$ mg N/m^3

C1 = .012 so that I' can fluctuate between practical limits of 4 (k=.05) and 50 (k=.6) J/cm²/h

C2 = .007 so that practical limits are .14 (k=.05) and .012 (k=.6)

C3 = .05 (added to C2, makes mortality vary between .19 and .06)

C4 = .012 so that respiration = 10% of p_{opt} in average conditions

C5 = .018 so that excretion = 15 % of p in average conditions

k_{max} = .6 corresponding to a p_{opt}/chlor.a = 25 (= 12.5 with uncorrected p_{opt}, cf. leakage).

K_s = 50 mg $N\text{-}NH_4^+/m^3$ (3.5 µgat N/l)

Q_{10} = 2.3

régénération rate of NH_4^+ from the sediment : 5 mg $N/m^2/h$ at 12°C .

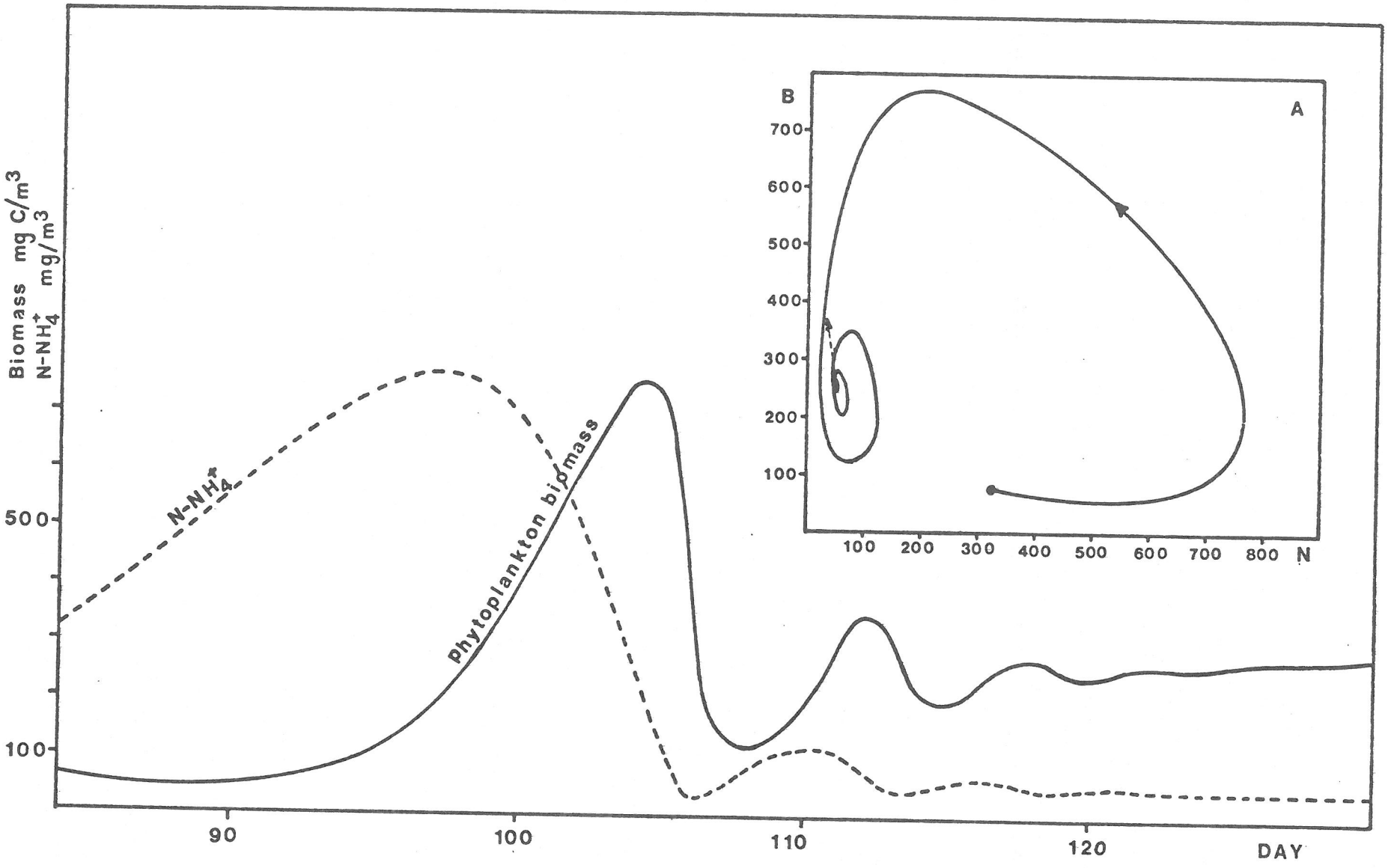

Biomass mg C/m3
N-NH4+ mg/m3
500
100
N-NH4+
phytoplankton biomass
90
100
110
120
DAY
B
A
700
600
500
400
300
200
100
100 200 300 400 500 600 700 800 N

FIG 1

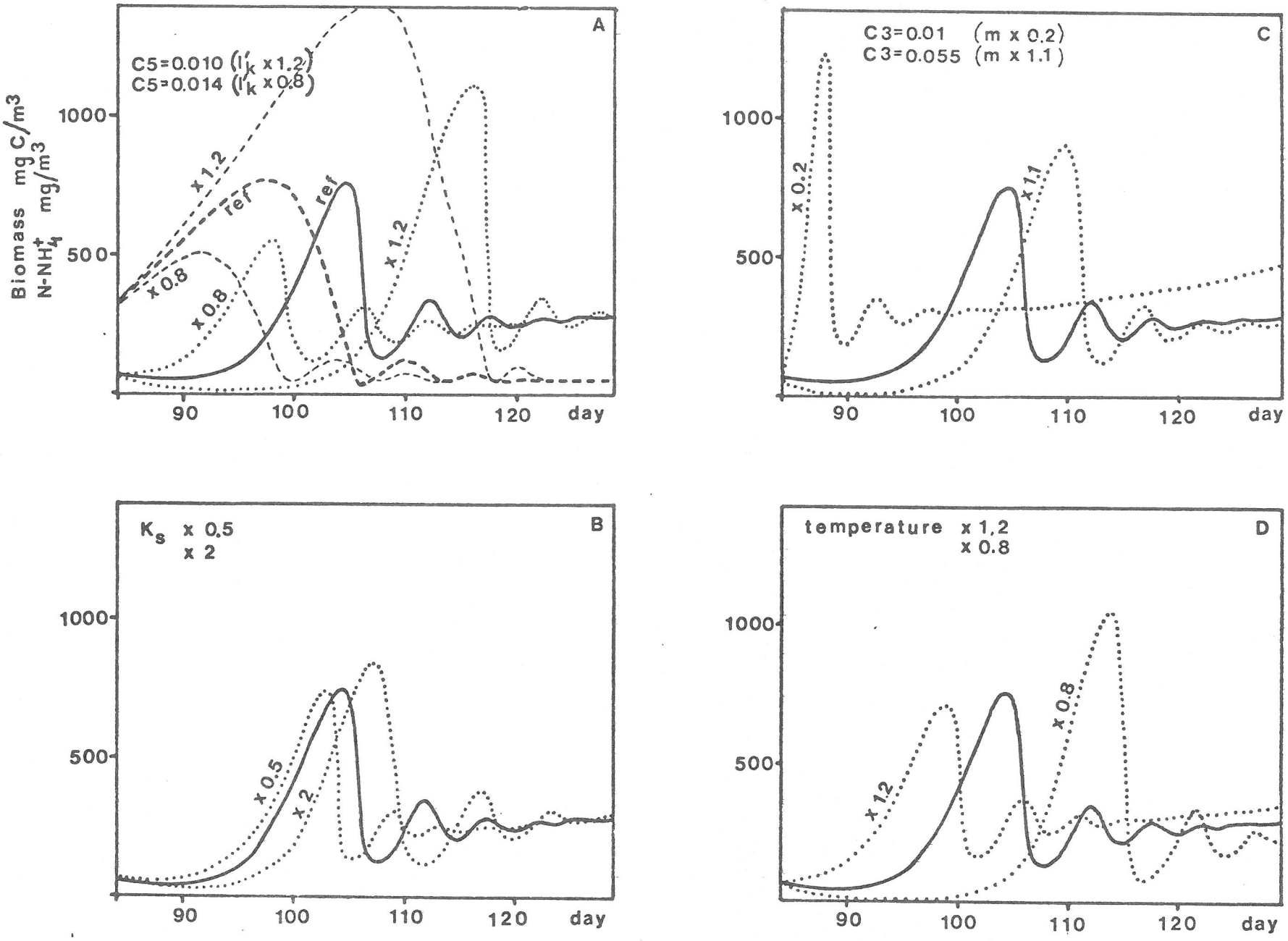
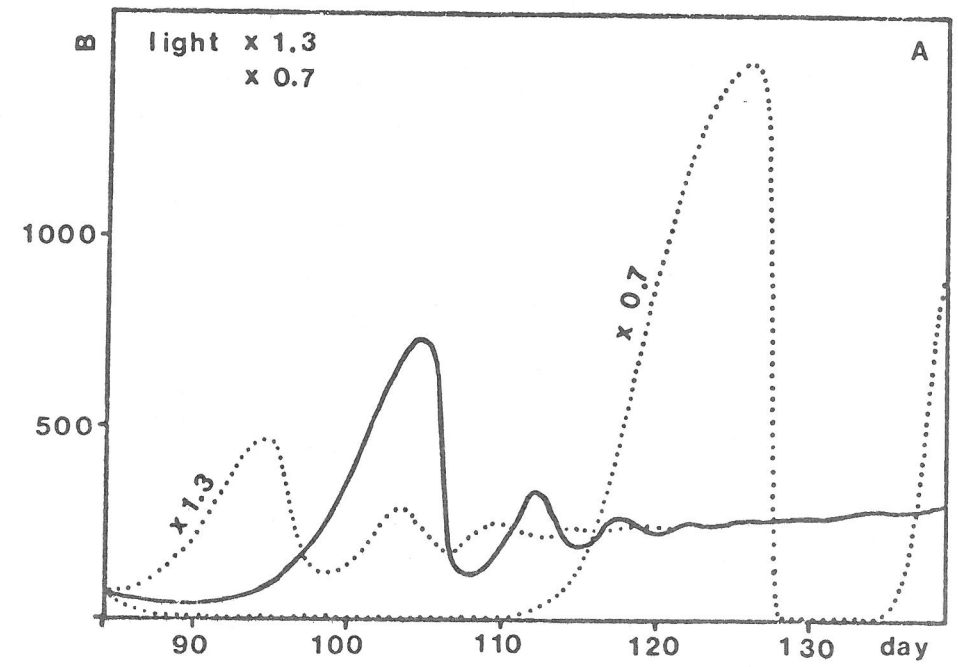
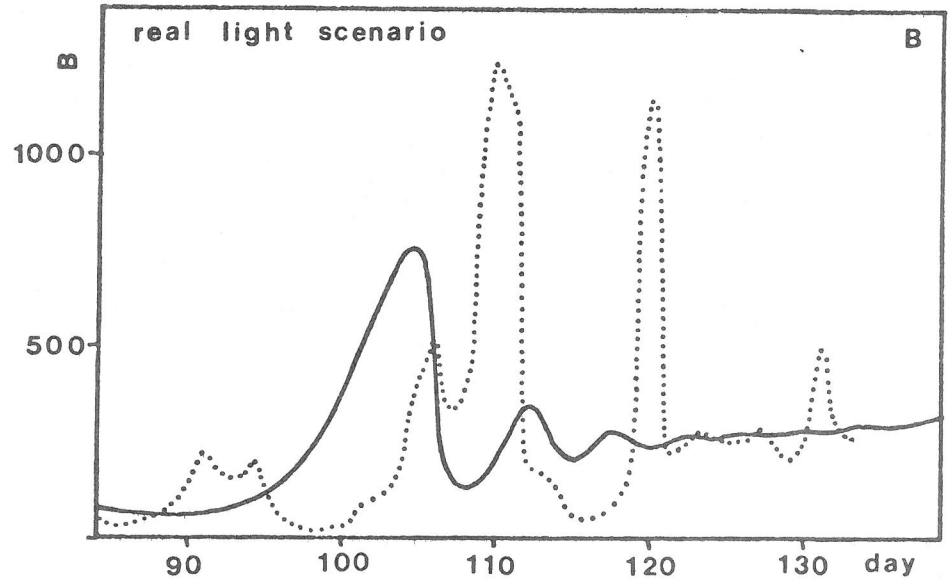

A
C5=0.010 (l'_k x 1.2)
C5=0.014 (l'_k x 0.8)
Biomass mg C/m3
N-NH4+ mg/m3
1000
500
x 1.2
ref
ref
x 0.8
x 0.8
x 1.2
90
100
110
120
day
C
C3=0.01 (m x 0.2)
C3=0.055 (m x 1.1)
1000
500
x 0.2
x 1.1
90
100
110
120
day
B
Ks x 0.5
x 2
1000
500
x 0.5
x 2
90
100
110
120
day
D
temperature x 1,2
x 0.8
1000
500
x 1.2
x 0.8
90
100
110
120
day

FIG 2


B
light x 1.3
x 0.7
A
1000
500
x 1.3
x 0.7
90
100
110
120
130
day


B
real light scenario
B
1000
500
90
100
110
120
130
day

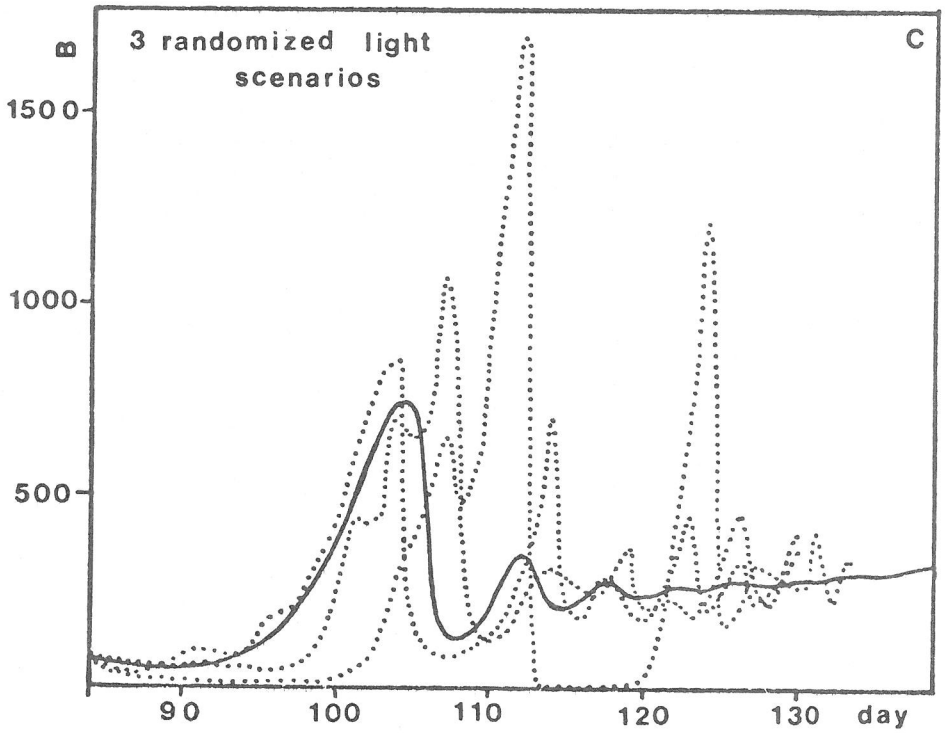

B
3 randomized light
scenarios
C
1500
1000
500
90
100
110
120
130
day

FIG 3

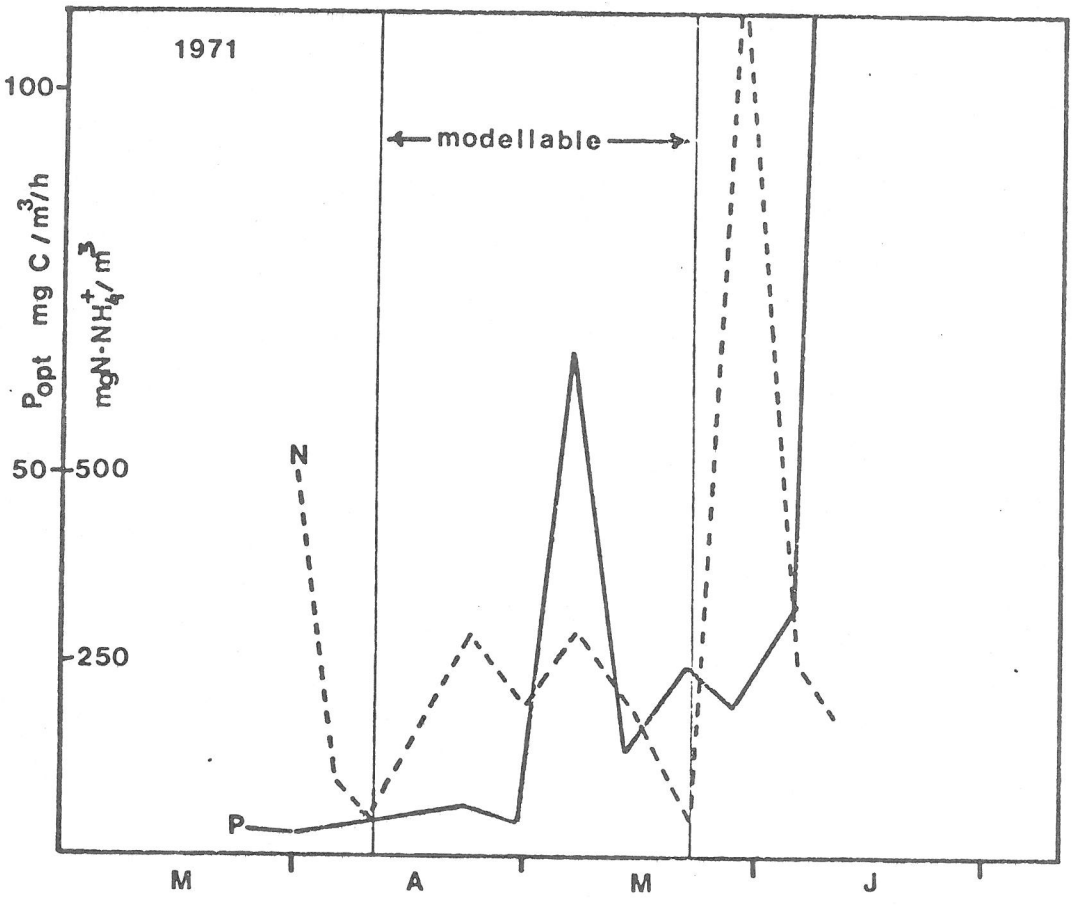

1971
100
modellable
P_{opt} mg C / m^3/h
$mgN\text{-}NH_4^+/m^3$
50
500
250
N
P
M
A
M
J

FIG 4